

mately related to the Tyranninæ, while morphologically it is intermediate between the latter and the Elaineinæ.

(4) The Tyranninæ form a natural section with which perhaps the Pitanginæ should be united.

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A DISCUSSION OF THE ORIGIN OF MIGRATION.

BY P. A. TAVERNER.

ONE of the first, if not the very first, phenomena of animate nature to be noticed by primeval man, must have been that of migration; and from that day to this it has been, to a greater or less extent, a subject of great interest to students. In the present day it has been approached from many different sides, and though many points have been pretty well cleared up, others are still enveloped in a haze through which the fundamental principles are but barely visible, while others still remain shrouded in a dense, impenetrable cloud of mystery.

The methods by which birds find their way to far distant points, the manner of their migrations, etc., lie without the scope of this paper, and will not be referred to here. Upon these points we all await the publication of the results of the investigations now in progress, when probably many obscure points will be cleared up.

Migration consists of two movements, one in the spring, away from the winter station; and the other in the fall, towards it again. The reason of the latter is self-evident. There is a lack of food. If they did not return in the fall they would perish of hunger, if not of cold. From general observations, it seems as if the former had a larger influence than the latter, and it is the northward movement that needs explanation. Why should a bird leave a warm land of plenty to journey to a country but half recovered from the frozen embraces of an arctic climate? It seems

improbable that the birds themselves realize why they migrate, or what benefits are to be thus gained or enemies escaped. When the proper season comes, "the spirit moves them," and they go or come, as the case may be. However instinctive their habit may now be, there must have been a time when migrations were intelligent movements, intended to escape some danger or secure some advantage; and through generations of repetition they have become fixed into hereditary habits, closely with reproduction and reproductive seasons. In time the two habits became so interdependent that the awakening of the sexual desires sympathetically affected the migratory instincts and caused restlessness and a desire that was only to be satisfied by the accomplishment of the same long journey that their progenitors had taken for generations.

Of the many theories that have been advanced to explain this question, I will mention a few that seem the most important and the most generally received. While advancing nothing absolutely new, I wish to call attention to one factor in the question that has not, in my estimation, been given its due importance, nor has it been recognized, as far as I am aware, that therein lie possibilities probably capable of producing all the phenomena of migrations as we now see them. Of this, more anon.

There is a theory extant, supported by W. K. Brooks in his 'Foundations of Zoölogy' that has received a considerable amount of attention. This ascribes migration to a desire to find nesting sites secure from arboreal Mammalia and Reptilia. This supposes, and perhaps correctly so, that the northern nesting stations are safer from these enemies than the tropical ones; though any one familiar with our northern woods, and acquainted with our ubiquitous red squirrel, may have good grounds for doubting the general statement, as far as it relates to mammals, at least.

There are certain facts of distribution, however, that this theory fails to explain, and which seem, indeed, to be in direct antagonism to it. Typical instances of this can be seen in the distribution and ranges of the families of Cuckoos and Doves. Also the occurrence of such an elaborate and careful nest builder as the Baltimore Oriole, as far north as the Transition fauna. Surely,

such a nest as this bird builds would be as secure from these enemies in the heart of the tropical forests as in the temperate ones. Therefore, safe nesting sites could not be the object of their migrating,—unless the peculiar form of nest was evolved after the migratory habit had been formed. This, however, does not seem to have been the case. Such a likeness is exhibited in the forms of the nests throughout the whole family, that we are forced to conclude that this type of nest was used by the common ancestor of *Icterus*, which must have been before the Baltimore Oriole became migratory.

The cuckoos and doves above mentioned, are notoriously careless nesters, and under this hypothesis, we would expect that migration would have been forced upon the whole of these families, or at least upon a considerable number of the species composing them. Contrary to this, we find that these are peculiarly tropical and subtropical families, and but a very small percentage of them ever get up into northern latitudes.

It may be held that the above cases are exceptions, caused by varying local conditions, but it still remains to be proved that the generality of tropical nesters take any greater nesting precautions than northern ones of the same class, as would assuredly be the case if the above were the correct solution of the problem. Furthermore, there are grave reasons, to which I will refer later, for doubting that inadequate nesting habits could ever be the cause of migrations.

A second theory, advanced under the auspices of Mr. Chas. Dixon, refers the movement to a natural desire of the individuals of a species to disperse during the breeding season, and draws attention to the fact that the bird population is more scattered during the breeding season than at other times. He utterly refutes the idea that adverse circumstances of either food, temperature, or enemies can force a bird to change its range, and cites instances of the Great Auk, Labrador Duck, and other species that have suffered extermination rather than forsake their accustomed habitat. Mr. Dixon evidently regards this dispersal as effecting a reduction in the density of the population. It certainly does result in this among the adult inhabitants, but it is open to question if we assume that the total population is

thus affected. His conclusion is apparently based upon the well known and indisputable fact that birds are harder to find during the breeding season than at other times. It must, however, be remembered that for each pair of breeding birds observed, there is somewhere about a nest full of young that are not seen at all. These young are of as much economic importance in reckoning population as the adults, and as such must be taken into consideration. On the whole, I doubt very much whether the bird population in the breeding season is any less per given unit of territory than at other times.

That migration is caused by a natural dispersal of the adults during the breeding season must be admitted. But this is begging the question. Migration is a dispersal; and conversely, this dispersal, as it manifests itself, is migration. The author fails to explain the cause of the natural dispersal. The object of this scattering may be seclusion, either for privacy or safety. If for privacy, it seems to defeat its own ends when such birds as the herons, swallows, and like gregarious nesters congregate in great communities to perform their marital duties. If safety is sought, it presupposes that all the safe nesting sites are monopolized by other species and the migrants are crowded out.

In our own country, we can readily see that but an infinitesimal fraction of possible sites are thus occupied. How rare it is for a nesting place to be used a second time by different individuals,—except in the case of woodpeckers' holes, where it is obvious that the supply is limited,—any field worker knows. If desirable forked branches, etc., were at such a high premium, this would occur frequently. If, then, the above is true in our own country, how much more must it be true in the tropical stations, where, though the population of both birds and their enemies is greatly increased, the luxuriant vegetation affords an infinitely greater number of desirable sites for nesting. Crowding in this sense seems impossible.

That individual birds cannot be driven from what they regard as their proper stations, may possibly be admitted; but that species cannot (when the adverse changes in surroundings take place gradually enough), is absurd. As far as I am aware, there are three principal ways by which geographical distribution can be

effected. One is the sudden irruption of a species, when it suddenly appears in numbers in a territory where it had been either extremely rare, or entirely absent. Examples of this are to be seen in the sudden occurrence of the Sand Grouse in Europe in 1888; the appearance of great flocks of Brünnich's Murre on Lakes Ontario and Erie, 1894-97, and the great movements occasionally noted in Lemmings. Of the underlying causes of these strange migrations, whether they are due to inner psychological or outer physical phenomena, we are ignorant. These strange overflows seem so erratic and abnormal in the light that invasions of this kind do not succeed in forming permanent settlements on the new grounds, that it would be reckless at present, to use them as a basis for theorizing, until all other means fail.

The second method is by a force exerted from within an established range; and the third, an attractive one acting from without. These two, however antagonistic as they may superficially seem, are, at root, one and the same. They are both caused by differences in the desirability of two stations. One is caused by a decrease in the desirability of a present, and the other by an increase of the same quality in an adjoining territory. They are but ratios of desirability, and can both be expressed by fractions whose values depend upon the relative, not the numerical size of their terms. If, then, attraction is but a phase of driving, and birds cannot be driven from their haunts, we are forced to discard all our present theories of geographical distribution and return to that of special creation, or found our science upon the unknown quantities of general irruption probably caused by psychological disturbances of whose origin and intent we are ignorant.

Ranges can be, have been, and in the course of time, must many times have been, changed by necessity when the changes in conditions occur slowly enough so that, though individuals may not, the whole species might have advanced or retreated. In this same manner, we know that even our forests have migrated back and forth across the continent before the face of the glacial ice, climbed mountains and descended valleys, though each individual tree or plant remained rooted for life to the spot where it originally sprouted. If plants can and have done this, I see no reason why birds could not also, as even in the most extreme case of local

attachment, a bird can never be as firmly fixed to its station as trees and plants are to theirs.

The cases of extermination cited are where the changes had come too suddenly, or where the species had become stereotyped or inflexible in habits and structure by too long and great success under peculiar conditions, and so lacked the elasticity of nature necessary to modify itself and its life to slight changes of environment.

A. R. Wallace has outlined another idea on the subject. He suggests, in 'Island Life,' that the migrants are in search of soft-bodied insects suitable for nestlings; that, as the season advances in the tropics, it becomes dryer and dryer, and such insects soon disappear. According to this view, it seems at first sight to be a seeking after food of a certain quality. Reduced to its lowest terms however, it appears as a very different matter, namely, a question of quantity. It is admitted that, even in the tropics, there is at least a short season when there are insects of a suitable quality for nestlings. That this season is long enough to raise birds, is evident, for many species closely related to our migrants successfully nest and raise their broods there. If all birds bred there at this same period, there would be suitable food there and migrations would be unnecessary. That they do not, is an indication that some other factor enters into the question, and it seems very probable that all birds breeding contemporaneously would exhaust the supply of such food. The question, then, is one of quantity more than quality.

It may be objected that each species requires its own special food at the critical nesting period, which may not be obtainable everywhere. Now, if there is any truth in our present evolutionary theory, great changes in food habits have occurred in all our species. But the new food supply must, in each and every case, have occurred before the habits and structure for utilizing it appeared. Therefore, food habits could never have originated migrations, though migration undoubtedly has had a great influence in modifying food habits.

It must be remembered also, that migration is a dangerous undertaking to a race. A journey covering thousands of miles, to be performed against innumerable enemies, both personal and

elementary, into a country just recovering from the rigors of winter, is a very hazardous solution of any problem. Especially must this have been true in the early days of the habit, when the races were much less adequately provided with hereditary experience and structure necessary for its successful conclusion. In this light, it seems highly improbable that anything short of the sternest necessity would favor the development of a habit so fraught with danger to the individuals of a species; and that, if any less hazardous solution were possible, it would have been taken advantage of.

The great diversity of food and nesting habits exhibited by closely allied species, shows how easily, comparatively speaking, these habits are modified. Therefore, if any peculiar nesting or food requirements menaced the welfare of tropical residents to the extent that must have been necessary to produce migration, it is reasonable to suppose these habits would have been altered to suit surroundings long before such a dangerous habit as migration could have been adopted.

The natural inference is that the problem was something that could be solved in no less hazardous way. For it would be much easier for birds to learn to build woven pensile nests at the end of long slender branches, or to adopt food that closely allied species found acceptable, than to create all the elaborate instincts, powers and structures necessary to enable them to traverse great stretches of country unguided, and in the face of meteorological disturbances, new enemies, strange foods, and all the dangers attendant upon migration. These grounds, then, alone seem sufficient to discredit any such phenomena as the foregoing, as prime causes in the origination of this habit.

The one cause that seems adequate to produce such great results, is that one which ultimately rules the whole animate world—the sufficiency of the food supply. Admitting that in the tropics there is, at any time, or more especially during the migration seasons, a lack of, or a severe struggle for food, and we have a necessity sufficiently imperative to cause the origin of any habit that it is possible to form. Mr. J. A. Allen, and others, have shown that the usual struggle for existence, always and everywhere intensely severe, is sufficient to cause an overflow into an

adjoining area whenever that area assumes conditions favorable for the support of an increased population. The return of spring causes the favorable conditions in the north, and the spring migration is the evidence of the overflow. The approach of winter influences life in the same manner, but the overflow, or migration is in the opposite direction.

Mr. Allen has very aptly applied the saying that "Nature abhors a vacuum," and suggests that migration is the only manner in which a zoölogical vacuum, in a country whose life-supporting capacity is a regularly fluctuating quantity, can be filled by non-hibernating animals.

That this view is correct, I do not think can be doubted, but there is another factor in the case that does not seem to have been generally perceived,—a fact that strengthens the foregoing reasoning manifold. True, Mr. Newton, in his 'Dictionary of Birds' has suggested it, but without apparently perceiving what a powerful factor it must prove in the case. I refer to the effect of the large increase of life in the breeding season, in an already thickly populated country, such as the southern stations must be just previous to the spring migration, coincident with the opening up for settlement of a vast adjoining and practically unoccupied territory, by the seasonal recession of the winter ice cap. Under the "Law of Malthus" we find a country to the south of us, populated to its fullest extent during the winter. Spring comes, and nearly every pair of birds has a nest full of young, requiring great quantities of food. The food demand must be increased to many times what it was before. There would, of course, be an increase in this food supply, due to the influence of spring, but it would not be in proportion to the demand. This inadequacy of the food supply is brought home to us very clearly if we reflect upon the fact that it takes the whole northern hemisphere to support the species in the summer that all through the winter were confined to a very limited territory; and that even then, during the time of greatest dispersal and food supply, the competition is always keen. Considering, then, that this great increase in population happens contemporaneously with an equal growth of the food producing territory due to the return of spring, it does not seem at all wonderful that the birds should migrate to utilize a

plentiful food supply and escape death by the causes attendant upon the evils of insufficient nourishment.

Migration, if the outcome of these phenomena, probably would have originated in the following manner. In the beginning of the breeding season, the competition would originate in the areas containing the earliest breeders, and would be severest in the most productive districts. Here the strongest species would soon drive out the weaker ones and the later breeders, which, having no parental ties to bind them to any one locality, would be more easily forced to leave than those already possessing nests — all other things, of course, being equal. These species, driven away, would encroach on others, forcing them out, in their turn, to trespass upon a wider circle of species. Thus the pressure arising from the congestion originating probably in the center of the winter residential area, would be felt to the farthest points of the populated territory. Any stringency of food supply invariably causes greater exertions on the part of the inhabitants, and hence wider ranging; and the slightest increase in sustaining power of adjoining lands would be immediately found and taken advantage of. As these species moved into the new country, their places would be quickly taken by those behind, and as the congestion was relieved, the impelling force would be constantly reinforced by the nesting of the later breeders as the season progressed.

The increase of population and life-supporting area would proceed regularly and evenly, so that the pressure would never exceed the relief. This nice balance would, of course, have been secured according to the laws of survival of the fittest — undesirable forms that would disturb the equilibrium, being either modified or eliminated.

Thus each species, crowded on by those behind, and enticed by the advance of those in front, would proceed onward until their own particular station had been reached. This point would be determined by one or more of several factors. The most obvious of these would be the failure of their particular food, the arrival of their nesting season, and the absence of superior competitors. When a species had reached this stage in its own particular migration, it would settle down and nest, and from then, to the end of its nidification period, would be fixed, and by its own increase

aid in driving forward those that had not yet found suitable conditions for nesting.

In the incipency of the migration habit, the individual movements would be small, perhaps originating in a pair of birds discovering an unexpected store of food on the side of a hill opposite their usual haunts. The birds that were bred here would find their way back the next year with greater ease than their parents did originally, and would be in a position to make further advances to the hill beyond. So each year, as the glacial ice receded, the territory suited for summer occupancy would be slightly enlarged, and the birds would each succeeding year, during the period of greatest stress, find sustenance a little to the northward of the preceding season's uttermost range.

The migratory movements and the differentiations of the breeding season are so closely connected that it is difficult to determine which originated first. Migration would delay breeding in the species that showed the slightest inclination towards the habit; and conversely, a delayed breeding season would actively assist the evolution of migration. The origination of both may have been simultaneous, though it is hard to imagine a time when some slight traces of migration would not have been beneficial to the races. At any rate, their effects would have been cumulative, each increasing and fixing the others. Once started, then, either or both would be rendered more and more pronounced, through natural selection, until the extreme limit profitable for each species was reached.

The gradual extension of the extreme summer range, as the glacial ice cap retreated, would most probably have been by means of the younger individuals, or birds in their first breeding season, of each species, as these would be weaker, and more easily driven than the older ones that would have become more attached to their local habitats. It seems universally true that young birds do not often return to breed in the immediate vicinity of the place where they are raised. There is a dispersing influence of some sort at work here. It is said that the older ones drive their offspring away from their hunting grounds when those offspring are able to take care of themselves. I cannot say from actual experience that they do this, but it seems so advantageous a

habit that its development is not only possible but very probable, and just what the student of evolution would expect.

This scattering of the younger individuals, however it was brought about, would then favor the extension of the migration range by the ones thus driven to wander from their accustomed haunts. As further substantiation of this, it is to be noticed that birds found far from their natural haunts are usually immature specimens.

A young bird on its first spring migration, would naturally return to the familiar place where it was raised. Being driven away from here, it would wander about until it found a suitable location for its own breeding — perhaps a mile, perhaps two, maybe less, away from its original home. The succeeding years, it would return to this new haunt, and the range of the species could be extended by its offspring. Thus, each bird would follow the route taken by its parents, and thus each point on a migration route would indicate the place that was once the ultimate goal of the migrations of its ancestors.

Migrations to true oceanic islands are more difficult to explain along these lines, but I do not think that they invalidate the reasoning in any way. Migrating birds certainly have wonderful, and as yet mysterious, senses of location and direction, and it is not too much to say that a bird, once it has traveled a certain journey, is usually able to find its way over the same path again. A pair of birds have only to be storm-blown to one of these isolated spots, breed there, and return with its progeny, to start a tendency in their offspring to migrate to the same place again. As long as the least tendency to an advantageous migration were started, natural selection would confirm, increase, and fix the habit firmly; and along with this, the new senses, structures and habits necessary to their accomplishment. It is unlikely, however, that this type of migration could be started until after certain powers and senses had been developed by migrations to other localities. They must, therefore, be regarded as secondary movements originally, though in some cases they have become now the prime or only migrations of the species by the extermination of all those individuals that adhered to the original routes.

The return movement in the fall is the same thing, nearly, as

the spring migration, but reversed. The shortage in food, however, is not caused, except indirectly, when the first migrants encroach upon those below them, by the increase of population, but by the direct failure of the food supply. It is perfectly evident that certain species must return south again, or stay and surely starve. The total population, however, of any area, cannot permanently remain greater than the number that can be sustained through the season of least food supply. During the height of the breeding season, there are many more birds than can be carried through the winter in the restricted southern stations, and if they are to return there again, the excess must be got rid of. Many of them are killed off at a very tender age — probably the great majority of them fail to survive the fledgling stage. Many more, young and inexperienced, must perish when first they leave the protecting influence of the parent's care. Others are battered about by the storms and destroyed by the perils incident to the fall migration. The few surplus that remain are subjected to a stricter and stricter process of selection as they reach more congested areas; and, in the end, the total population fits into its place in the winter quarters, to the extreme limit of the supporting powers of the land.

These migrations, in their earliest stages, must then have originated in a conscious seeking for food — not special food, but any food that would support them. Accidental wanderings taught them where to find it, and experience suggested their return there on the first approach of a stringency in the food supplies. In course of time, the movement became habitual, and generations of repetition rendered it instinctive. Instinct, having the same relation to judgment as automatic machinery has to ordinary mechanism, would be favored through natural selection; and as the birds acquired the peculiar powers necessary, migrations assumed all the varied phenomena that they exhibit to-day.